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# Density dependence and stochastic variation in a newly established population of a small songbird

Bernt-Erik Sæther, Steinar Engen, Russell Lande, Christiaan Both and Marcel E. Visser

Sæther, B.-E., Engen, S., Lande, R., Both, C. and Visser, M. E. 2002. Density dependence and stochastic variation in a newly established population of a small songbird. – *Oikos* 99: 331–337.

Models describing fluctuations in population size should include both density dependence and stochastic effects. We examine the relative contribution of variation in parameters of the expected dynamics as well as demographic and environmental stochasticity to fluctuations in a population of a small passerine bird, the pied flycatcher, that was newly established in a Dutch study area. Using the theta-logistic model of density regulation, we demonstrate that the estimated quasi-stationary distribution including demographic stochasticity is close to the stationary distribution ignoring demographic stochasticity, indicating a long expected time to extinction. We also show that the variance in the estimated quasi-stationary distribution is especially sensitive to variation in the density regulation function. Reliable population projections must therefore account for uncertainties in parameter estimates which we do by using the population prediction interval (PPI). After 2 years the width of the 90% PPI was already larger than the corresponding estimated range of variation in the quasi-stationary distribution. More precise prediction of future population size than can be derived from the quasi-stationary distribution could only be made for a time span less than about five years.

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Quantifying the relative contribution of density dependence and stochastic factors has been a central question in the ecological literature (see reviews in Sinclair 1989, Turchin 1995). In the middle of the 1970s it was realized that small changes in some essential parameters of deterministic density dependent models could produce large changes in population dynamics (May 1976). Adding stochasticity to these models further complicates the dynamics (May 1973, Turelli 1977, Leigh 1981) and introduces the possibility of extinction (Lande and Orzack 1988, Lande 1993, 1998). Thus, a proper understanding of avian population dynamics, including determination of the size of a viable population, requires quantification of the deterministic compo-

nents influencing the expected dynamics as well as the stochastic factors causing fluctuations in population size.

Here we define the strength of density dependence as the negative elasticity of population growth rate per generation with respect to change in population size,  $D = -\partial \ln \lambda^T / \partial \ln N$  (Lande et al. 2002), where  $\lambda$  is the population growth rate,  $N$  is the population size, and  $T$  is the generation time, defined as the mean age of mothers of the newborns when the population is in a stable age distribution. Because we are analyzing population data on a small passerine bird, we assume an average age at maturity of females of one year, and negligible effects of age-specific demographic variation

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on the population growth rate. We then compute the strength of density dependence  $D$  evaluated at the equilibrium population size ( $K$ ) for the expected dynamics (where  $\lambda = 1$ ) as  $D = -T(\partial \ln \lambda / \partial \ln N) = T\gamma$ , where the generation time is  $T = 1/(1 - s)$  and  $s$  is the adult annual survival rate at equilibrium. The parameter  $\gamma$  gives the expected rate of annual return to equilibrium, corresponding to the time scale for return to equilibrium of  $1/\gamma$  years (Lande et al. in press). This will depend on the form of density regulation (May 1981). Here we use the theta-logistic model of density regulation (Gilpin and Ayala 1973, Gilpin et al. 1976, Diserud and Engen 2000), which encompasses a wide range of density regulation functions depending on the single parameter  $\theta$ , including the familiar Gompertz ( $\theta = 0$ ) and logistic ( $\theta = 1$ ) models. This model has the advantage of relatively well understood statistical properties (Diserud and Engen 2000, Sæther et al. 2000a) that allow us to characterize population fluctuations, while avoiding problems such as increasing variance estimates with the length of census period (Pimm 1991).

Environmental stochasticity expressed by the environmental variance  $\sigma_e^2$  is caused by changes in the physical or biological environment that affecting all individuals in a population in a similar way. This has been shown to strongly influence the dynamics of vertebrate populations (Lande et al. in press). In addition, demographic stochasticity expressed by the demographic variance  $\sigma_d^2$  (generated by independent chance events in individual reproduction and survival) will also affect population dynamics, especially at small population sizes, generating both stochastic fluctuations and a decrement of the long-run growth rate of the population (Lande 1998). Under the influence of demographic stochasticity, the population process will no longer be stationary and extinction will inevitably occur. The magnitude of demographic stochasticity is likely to strongly influence the expected time to extinction (Engen et al. 2001, Lande et al. in press). The quasi-stationary distribution of population sizes, including the effects of demographic stochasticity, can be approximated by using diffusion models (Karlin and Taylor 1981).

An important challenge for ecologists is to develop accurate population projections. This not only requires modeling the expected dynamics and stochasticity but also evaluation of uncertainties in the parameter estimates. We incorporate these effects into the population prediction interval (PPI), which is a stochastic interval that includes the unknown future population size with probability  $(1 - \alpha)$  (Dennis et al. 1991, Engen and Sæther 2000, Engen et al. 2001). The interpretation of a prediction interval is the same as for a confidence interval (Sæther and Engen 2002a), except that we draw inference about a stochastic quantity rather than a parameter. The width of the PPI increases with increas-

ing stochasticity (Heyde and Cohen 1985) and with increasing uncertainty in parameter estimates.

The purpose of the present study is to compare the relative contribution of deterministic and stochastic factors to fluctuations in the size of a newly introduced population of a small, cavity nesting passerine, the pied flycatcher (*Ficedula hypoleuca*). Our population has fluctuated over a wide range of sizes, providing an unusual opportunity to obtain estimates of parameters that are often difficult to estimate in stationary time series such as the specific population growth rate, the density regulation function, and demographic and environmental stochasticity (Aanes et al. 2002). Utilizing the concept of PPI, we then predict future population sizes, including both stochastic factors and uncertainties in the population parameters. This allows us to address the question of how far ahead we can accurately project future population fluctuations more precisely than those that can be derived from the quasi-stationary distribution of population size.

## Population model

We model fluctuations in the logarithm of the population size,  $X = \ln N$ , where  $N$  is the population size at time  $t$ . Let  $\Delta X = \ln(N + \Delta N) - \ln(N)$ . The expectation of  $\Delta X$  is assumed to have the form  $\ln \lambda(N) = \bar{r}[1 - (N/K)^\theta]$  (Sæther et al. 2000a), where  $\lambda(N)$  is the population growth rate in the absence of stochasticity,  $K$  is the carrying capacity,  $\bar{r}$  the mean specific growth rate, and  $\theta$  describes the form of density regulation. This is often called the theta-logistic model (Gilpin and Ayala 1973) and may alternatively be written as  $\ln \lambda = r_1[1 - (N^\theta - 1)/(K^\theta - 1)]$ , where  $r_1 = \bar{r}(1 - K^{-\theta})$  is the specific growth rate when  $N = 1$ . It is a valid model for negative as well as positive values of  $\theta$ . For  $\theta = 0$  we use the limiting form  $\ln \lambda(N) = r_1(1 - \ln N / \ln K)$ . Taking the derivative with respect to  $\ln N$ , we find

$$\gamma(N) = -\frac{\partial \ln \lambda}{\partial \ln N} = \frac{r_1 \theta}{\lambda(N)} \frac{N^\theta}{K^\theta - 1}$$

and at  $N = K$  with  $\lambda(K) = 1$  we have  $\gamma(K) = \bar{r}\theta$  (Sæther et al. 2000a). Thus, strong density dependence occurs at  $K$  when the specific population growth rate is high and/or for large values of  $\theta$ . We also see that when  $\theta = 0$  (Gompertz density regulation)  $\gamma(K) = r_1 / \ln K$  and when  $\theta = 1$  (logistic density regulation)  $\gamma(K) = \bar{r}$ .

Now we model  $\Delta X$  with stochastic density-independent growth rate and deterministic density dependence so that

$$\Delta X = r_1(t) - \bar{r}_1 \frac{e^{X\theta} - 1}{K^\theta - 1},$$

where  $r_1(t)$  is normal with mean  $\bar{r}_1$  and variance  $\text{var}[r_1(t)] = \sigma_e^2 + \sigma_d^2 e^{-X}$  (Lande 1993). Assuming that  $\Delta X$  is small, we can use a diffusion approximation for  $X$  (Karlin and Taylor 1981, Diserud and Engen 2000) with infinitesimal mean

$$m(X) = r_1 \left[ 1 - \frac{e^{X\theta} - 1}{K^\theta - 1} \right]$$

and infinitesimal variance  $v(X) = \sigma_e^2 + \sigma_d^2 e^{-X}$ . The quasi-stationary distribution is

$$f(X; X_0) = G(X, X_0) / \int_1^\infty G(X, X_0) du$$

(Lande et al. 1995). Here  $G(X, X_0)$  is called the Green function or the sojourn time starting from an initial size  $X_0$ . The Green function expresses the expected cumulative time spent at each population size before extinction (Karlin and Taylor 1981). Assuming that the population size is so large that  $\sigma_d^2$  can be ignored, the diffusion approximation to the variance of the stationary distribution of  $N$  in the theta-logistic model is

$$\sigma_N^2 = \frac{K^2 \Gamma[(\alpha + 2)/\theta]}{[(\alpha + 1)/\theta]^{2/\theta} \Gamma(\alpha/\theta)},$$

where  $\alpha = (2r_1/\sigma_e^2)(1 - K^{-\theta}) - 1$  and  $\Gamma$  denotes the gamma function (Diserud and Engen 2000).

## Methods

### Study population

This study was conducted in a coniferous-dominated mixed forest in the Hoge Veluwe area, central Netherlands. The size of the study area was 290 ha until 1972, and in 1973 it was reduced to 179 ha. Since 1955 more than 200 nest boxes have been available although many

of those were already occupied by great tits (*Parus major*) and blue tits (*P. caeruleus*) at the time pied flycatchers arrive in spring. Data on reproduction and survival were obtained through weekly inspection of nest boxes, and banding of chicks and adults with uniquely numbered aluminum rings.

The pied flycatcher established itself in the study area in 1959, when two pairs bred. One pair was recorded in 1962 and the species has since then bred continuously each year in the study area (Fig. 1). The establishment and increase of the population was associated with a large-scale range expansion at the Western border of the species' breeding range (Lundberg and Alatalo 1992). For a closer description of the study population, see Both et al. (in prep.).

### Parameter estimation

The demographic variance in each year  $t$  was estimated (Engen et al. 1998) as the weighted mean across years of  $\sigma_d^2(t) = 1/(n-1) \sum (R_i - \bar{R})^2$ , where  $R_i$  is the contribution of an individual  $i$  to the next generation,  $\bar{R}$  the mean contribution of the individuals and  $n$  is the number of recorded contributions in year  $t$ . The total contribution of a female  $i$  in year  $t$  ( $R_i$ ) is the number of female offspring born during the year that survive for at least one year plus 1 if the female survives to the next year (Sæther et al. 1998). We excluded the year 1994 from the analyses because of strongly reduced recapture rates the following year. The other parameters were estimated by least square techniques as described elsewhere (Sæther et al. 2000a). Uncertainties in the parameters were determined by parametric bootstrapping (Efron and Tibshirani 1993).

Significance testing of estimates of  $\theta$  was performed by simulating the process under two null hypotheses that  $\theta = 1$  (logistic density regulation) or 0 (Gompertz density regulation).

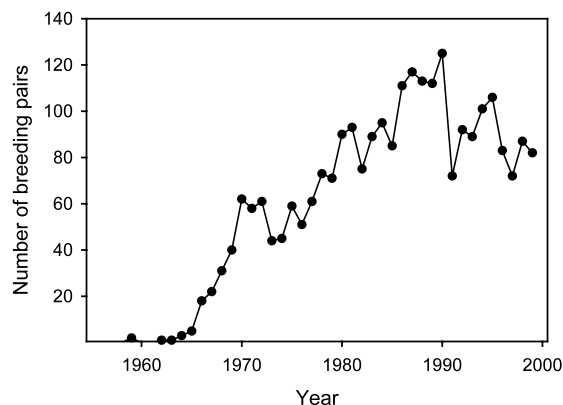


Fig. 1. The fluctuations in the number of breeding females in the pied flycatcher population at Hoge Veluwe, Netherlands.

### Population prediction interval (PPI)

We evaluated the prediction intervals for population size (PPI) at each time by stochastic simulations (Efron and Tibshirani 1993). We simulate the process using each bootstrap replicate of the parameter values. The upper end of the  $(1 - \alpha)$  prediction interval at time  $t$  then ranges upward from the corresponding quantile obtained from the simulations (Engen et al. 2001). This method for evaluating the population prediction interval is not exact. Stochastic simulations do however show (Sæther et al. 2000a, Engen et al. 2001) that the coverage is often quite close to the theoretical probabilities.

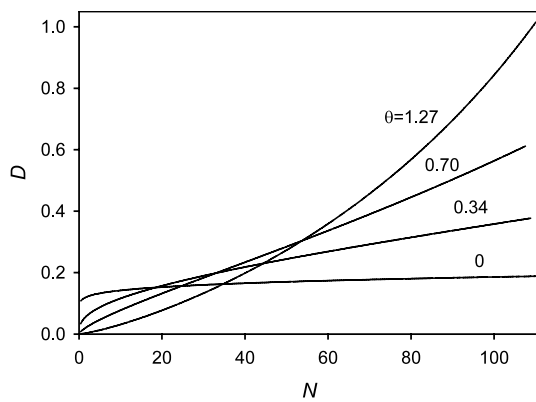


Fig. 2. The strength of density dependence  $D = \gamma(1 - s)$  in relation to population size  $N$  for different values of  $\theta$  in the theta-logistic model. The annual survival rate of adult females was  $s = 0.28$  (Both et al. in prep.).  $\theta = 0.34$  and  $\theta = 1.27$  represent the lower and upper 25% quantile of the bootstrap distribution of  $\theta$  (see Fig. 3A), whereas  $\theta = 0$  represents a Gompertz type of density regulation. For  $\theta = 0$  the estimates of the other parameters were  $r_1 = 0.605$ ,  $K = 95.15$  and  $\sigma_e^2 = 0.0416$ , for  $\theta = 0.34$   $r_1 = 0.546$ ,  $K = 86.93$  and  $\sigma_e^2 = 0.0376$  and for  $\theta = 1.27$   $r_1 = 0.378$ ,  $K = 88.31$  and  $\sigma_e^2 = 0.0376$ .

## Results

As is the case in several small songbird populations (Sæther et al. 1998, 2000a, b, Engen et al. 2001), a high proportion (63.2%) of the breeding attempts failed to contribute to subsequent generations. Similarly, the pooled probability distribution of 1, 2 or 3 female recruits was 0.326, 0.037 and 0.005, respectively (with  $\Sigma R_i = 2117$ ). Based on the annual variation in these distributions and fluctuations in population size, we obtained an estimate of the demographic variance  $\hat{\sigma}_d^2 = 0.33$  and the environmental variance  $\hat{\sigma}_e^2 = 0.0356$ . Neither of the two stochastic components was significantly correlated with population size (correlation = 0.07,  $n = 32$ ,  $P > 0.1$  and correlation = -0.07,  $n = 34$ ,  $P > 0.1$  for the demographic and environmental variance, respectively). Furthermore, annual variation in the point estimates of the two stochastic components was also uncorrelated (correlation = 0.24,  $n = 32$ ,  $P > 0.1$ ).

At small population sizes the pied flycatcher population growth rate was high ( $\hat{r}_1 = 0.474$ ). The estimate of  $\theta$  was 0.696, giving  $\hat{\gamma} = 0.375$  at the carrying capacity ( $\hat{K} = 86$  pairs). Fig. 2 plots  $D = \gamma/(1 - s)$  as a function of  $N$ , showing that the strength of density dependence  $D$  increases with population size.

Large uncertainties were found in the estimates of  $\theta$  (Fig. 3A, SD = 0.81). Accordingly, the estimated  $\hat{\theta} = 0.696$  was not significantly different from either  $\theta = 0$  or  $\theta = 1$  ( $P > 0.2$ ). Among the other three parameters  $K$  was estimated with greatest accuracy (CV = 0.14, Fig. 3B), whereas the uncertainties in the estimates of  $\sigma_e^2$

and  $r_1$  were larger (CV = 0.41 and 0.29, respectively, Fig. 3C, D).

The lower and upper 0.5%-quantile of the stationary distribution of population sizes, using the parameter

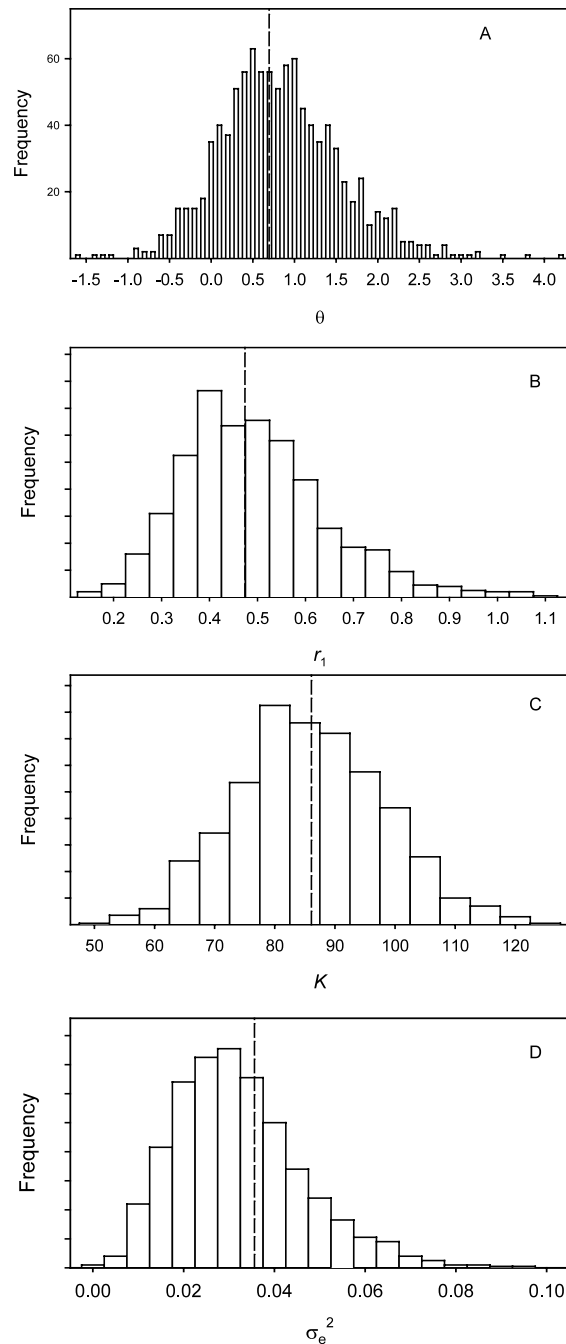


Fig. 3. The distribution of the bootstrap replicates of  $\theta$  that describes the form of the density regulation (A), and the bootstrap distributions of  $r_1$  (B), carrying capacity  $K$  (C) and environmental stochasticity  $\sigma_e^2$  (D) for  $\theta = 0.696$ . Dashed lines indicate the estimated values of the parameters.

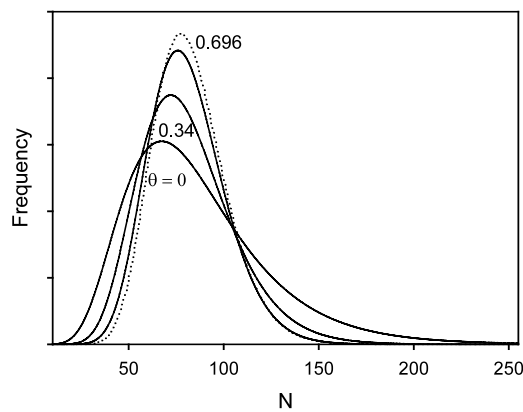


Fig. 4. The stationary (dotted line) and quasi-stationary distributions of the size of the population of pied flycatcher computed for different values of  $\theta$  in the theta logistic model. Parameter values as in Fig. 2.

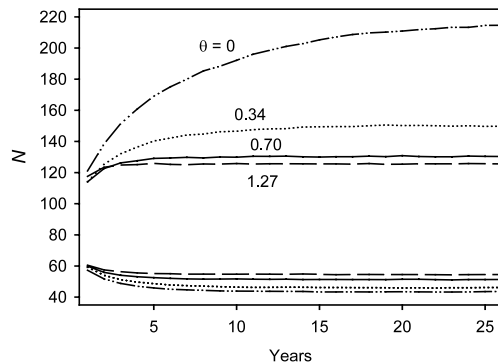


Fig. 5. The 90% population prediction interval (PPI) for the pied flycatcher for different values of the density regulation  $\theta$ . Parameter values as in Fig. 2.

estimates of  $\theta$ ,  $r_1$ ,  $K$  and  $\sigma_e^2$ , was 43 and 141 pairs, respectively (Fig. 4). Thus, we expect that 99% of all future population fluctuations will occur within this range of variation in population size, assuming no demographic stochasticity. The quasi-stationary distribution (with  $\sigma_d^2$  included) was similar, but with a slightly higher proportion of the distribution located at smaller population sizes. This shows that this population is unlikely to go extinct in the near future [ $\log_{10}$  (expected years to extinction starting at  $K$ ) = 14.847]. The high immigration rates recorded at small population sizes (Both et al. in prep.) indicate that this actually underestimates the expected time to extinction in the absence of nonstationary environmental changes.

To examine the sensitivity of the variance in the quasi-stationary distribution of population sizes to variation in the parameter estimates we used the lower and upper 25% quantile from the distribution of the bootstrap replicates of  $r_1$  and  $\sigma_e^2$ , respectively (Fig. 3). Both changes affect the variance in the stationary distribution. Reducing  $r_1$  increased the standard deviation in

the distribution from 20.08 to 22.86 pairs, whereas increasing  $\sigma_e^2$  increased the standard deviation to 21.57 pairs. Correspondingly, the  $\log_{10}$  of the expected years to extinction decreased from 14.847 to 13.417 with this increase in  $\sigma_e^2$ , and to 11.210 with this decrease in  $r_1$ .

The form of the density regulation function (given by  $\theta$ ) strongly affected the quasi-stationary distribution of population sizes. When choosing the commonly used (e.g. Royama 1992) linear model on log scale ( $\theta = 0$ ), we get an approximate lognormal quasi-stationary distribution (Fig. 4), associated with the strength of density dependence being approximately independent of  $N$  (Fig. 2). This increases the variation in population size in comparison to that for the estimated  $\theta$ , resulting in a large increase in the standard deviation in the quasi-stationary distribution from 20.08 to 37.66 pairs for  $\theta = 0$ . As a consequence, the expected time to extinction was strongly reduced,  $\log_{10}$  (expected years to extinction) = 10.59. In contrast, using the upper 25 quantile in the bootstrap distribution of  $\theta$  ( $\theta = 1.27$ ), the variance in the quasi-stationary distribution decreased ( $SD = 17.99$ ) because of a large increase in the strength of density dependence  $D$  with  $N$  (Fig. 2). Thus, the form of the density-regulation function has a major impact on the range of fluctuations in population size.

The width of the 90% PPI became stable after a short period (Fig. 5), ranging from 51 to 131 pairs. However, the PPI was sensitive to the choice of  $\theta$ . The width of the PPI increased with decreasing values of  $\theta$  because the population was predicted to spend a larger proportion of the time at sizes far above  $K$  (Fig. 5). Thus, accurate predictions of future population fluctuations are strongly dependent on accurate estimates of the form of density regulation  $\theta$ .

## Discussion

The first pied flycatchers were recorded in the study area in 1959 (Fig. 1). This study demonstrates that a viable population of pied flycatcher, where fluctuations occur within a certain range of population sizes through density-dependent regulation, can be formed within only three to four decades after initial colonization (Fig. 4 and 5). The variance of this quasi-stationary distribution is determined by the parameters influencing the expected dynamics as well as environmental stochasticity.

Estimates of both demographic and environmental stochasticity were smaller in the pied flycatcher than in three other small passerines: the great tit (Sæther et al. 1998), the dipper (*Cinclus cinclus*) and the song sparrow (*Melospiza melodia*) (Tufto et al. 2000). However, in all species the stochastic components of the population dynamics are large (e.g. Fig. 3D), and thus must be estimated and modeled to obtain a proper understanding of the population dynamics of small passerines.

Even though the demographic stochasticity was high in the pied flycatcher population, the quasi-stationary distribution using  $\sigma_d^2 > 0$  was similar to the stationary distribution obtained for  $\sigma_d^2 = 0$  with a small proportion of the probability density at low population sizes (Fig. 4), resulting in a very long expected time to extinction. This is mainly the result of the large specific growth rate in the population ( $\bar{r}_1 = 0.474$ ) that may be due to larger immigration rates and higher recruitment rates at smaller densities (Both et al. in prep.). This prevents the population from remaining at smaller population sizes for longer periods of time. Furthermore, the parameter  $\gamma(K) = \bar{r}\theta$  was estimated as 0.375. Consequently, the time scale for return to equilibrium ( $1/\gamma$ ) is rather short (on the order of 3 years), and the population is likely to frequently cross the carrying capacity  $\bar{K} = 86$  (Fig. 4).

The quasi-stationary distribution is strongly affected by the form of density regulation depending on  $\theta$ . In many analyses of density dependence in population time series a loglinear model of density regulation is chosen a priori (e.g. Royama 1992). This corresponds to  $\theta = 0$  in the theta-logistic model. Such a density regulation function gives an approximate (exact for the diffusion with  $\sigma_d^2 = 0$ ) lognormal quasi-stationary distribution (Fig. 4) that differs from the estimated quasi-stationary distribution (computed using the estimates of  $\theta$ ,  $r_1$ ,  $K$  and  $\sigma_e^2$ ) in having a much higher proportion of the probability density at very large population sizes. This difference is due to the strength of density dependence  $D$  being independent of population size for  $\theta = 0$ , but increasing with  $N$  for  $\theta > 0$  (Fig. 2). Values of  $\theta$  larger than 0 seem to be typical for small temperate songbird populations (Sæther et al. 1998, 2000a, b, 2002, Tufto et al. 2000, Sæther and Engen 2002b), indicating that the strength of density dependence increases with population size (Fig. 2). The form of the density regulation function should therefore be carefully considered when interpreting the results of population dynamic analyses of such species.

The difficulties in estimating  $\theta$  may be related to demographic characteristics of the pied flycatcher that also are typical for the demography of many small passerines. In the pied flycatcher, density dependence in reproduction only appears at very high densities (Tompa 1967, Stenning et al. 1988, Both 2000), whereas no density dependence in either juvenile or adult survival rate was recorded in the present population (Both et al. in prep.). As a consequence, the reduced growth rates at high densities were due to a decrease in the recruitment rate, possibly related to increased competition between juveniles and adults for access to breeding sites (Both et al. in prep.). This is further supported by a higher age of first breeding in years with high densities (Both et al. in prep.). This suggests that reliable estimates of the density-regulation function require data from years when the population size is far above the carrying capacity.

The pied flycatcher population in Hoge Veluwe was continuously studied for 38 years, which is a long period compared to the length of most ecological field studies. During this study the fluctuations covered a wide range of population sizes, which facilitates the reliable estimation of population parameters. In spite of this, the uncertainty in several of the parameters was quite large (Fig. 3). In combination with the stochastic effects on the population dynamics, precise prediction of future population size is difficult even for a short time span (Fig. 5). If the precision in the population projections was unaffected by uncertainty in the parameter estimates, we would expect the width of the prediction interval to be approximately similar to the range of variation in the quasi-stationary distribution of population sizes. However, assuming no uncertainties in the parameter estimates the width of the 90% PPI after 2 years (Fig. 5) was already larger than the corresponding range (between the 5th and 95th percentile) of the estimated quasi-stationary distribution of population size (Fig. 4). Furthermore, when the width of the 90% PPI became stable after 5 years (Fig. 5), in accordance with time scale for a return to equilibrium of about 3 years, it was 21% larger than the range of the estimated quasi-stationary distribution of population size (5th percentile: 51 pairs, 95th percentile: 117 pairs, Fig. 4). This indicates that our ability to predict the range of variation in the size of this pied flycatcher population was influenced by stochastic effects and deterministic components in the dynamics as well as uncertainties in the parameter estimates. Thus, development of population projections beyond a short time span will be difficult for small passerines such as the pied flycatcher even when long time series are available.

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